THE LARVA OF *CERMA* HÜBNER AND ITS ENIGMATIC LINKAGES TO THE ACRONICTINAE (LEPIDOPTERA: NOCTUIDAE)

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Abstract.—The larva of *Cerma cerintha* (Treitschke) is described and figured and compared to that of *C. cora* Hübner. Both *C. cerintha and C. cora* are illustrated with photographs. The presence of only two SV setae on A1 and fully-developed prolegs on A3–A6 suggest that *Cerma* is neither an Acontiinae nor Eustrotiinae, the two subfamilies in which the genus is classified in modern taxonomic works. Morphological and behavioral similarities shared with *Acronicta fragilis* (Guenée), *Harrisimemna trisignata* (Walker), and other acronictines are discussed: *Cerma* Hübner and *Harrisimemna* Grote appear to have an especially close association. If *Cerma* proves to be an acronictine, its membership will call into question two of the strongest larval characters that have been used to diagnose the dagger moth subfamily: i.e., the presence of secondary setae and two or more setae on the L3 pinaculum on A1–A8. An alternative interpretation for the numbering of the L seta on the ninth segment is suggested. It is hypothesized that the aposematic coloration and alarm posture of *Cerma* are functionally linked to defensive secretions released from the larva's enlarged cervical gland.

Key Words: wood tunneling, alarm response, cervical gland, Comachara, Harrisimemna, Polygrammate, aposematic

The common, handsomely-colored adults of Cerma cerintha (Treitschke) are familiar to most eastern moth collectors. The forewings, a muddled mix of white and gray, give the resting moth the appearance of a bird dropping. Largely because of its coloration, Cerma cerintha has been classified in or near the Acontiinae [it was even described in the nominate genus Acontia Ochsenheimer by Treitschke (1826)]. For many years two (of the three) North American species of Cerma Hübner were not recognized as congeners. In McDunnough's (1938) checklist, C. cora Hübner, the type species of the genus, was treated as a cuculline. In addition to $C_{\rm c}$

cora, McDunnough's concept of Cerma included all described members of the brvophiline genus Cryphia Hübner; C. cerintha was left in Guenée's Chamyris in the Acontiinae-a position unchanged from earlier taxonomic works (e.g., Dyar et al. 1902 and Holland 1903). Forbes (1954) moved C. cerintha into Cerma, excluded all Cryphia, and placed the genus near Ogdoconta Butler and Perigea Guenée (= Condica Walker) in his "isolated Acronyctine genera." (At that time, Forbes' concept of the Acronyctine [sic] was extremely broad, encompassing members from ten of Fibiger and Latrifid subfamilies.) fontaine's 2005 Crumb (1956) placed C. cerintha in his

Lithacodiinae—an unnatural assemblage with little allegiance to one another, held together, in part, by the relative position of the stemmata. Most recently *Cerma* has been classified as an acontiine (Franclemont and Todd 1983) or eustrotiine (Fibiger and Lafontaine 2005). Here I describe the larva of *C. cerintha* and identify characters that suggest that *Cerma* might be best placed in the Acronictinae, near to or as the sister of *Harrisimenna* Grote.

MATERIALS AND METHODS

The description of C. cerintha is based on four mature larvae from a single ex ova cohort reared on Prunus serotina Ehrh. (Rosaceae). Data for the mother: NY: Albany Co., Pine Bush, 42°42'45"N and 73°52'53"W, 25 July 1981, T. L. McCabe. Larvae of Cerma cora (NY: Albany Co., Pine Bush, 42°42'45"N and 73°52′53″W, mother taken 8 July 1988. T. L. McCabe, reared on Prunus pensylvanica L. (Rosaceae), n=5) and Harrisimemna trisignata (NY: Hamilton Co., Pine Bush, 43°45'30"N and 74°10'14"W, mother taken 1 August, 1980, T. L. McCabe, reared on Spiraea latifolia (Ait.) Borkh. (Rosaceae), n=4) were also examined. Larval specimens are deposited at the New York State Museum. Albany.

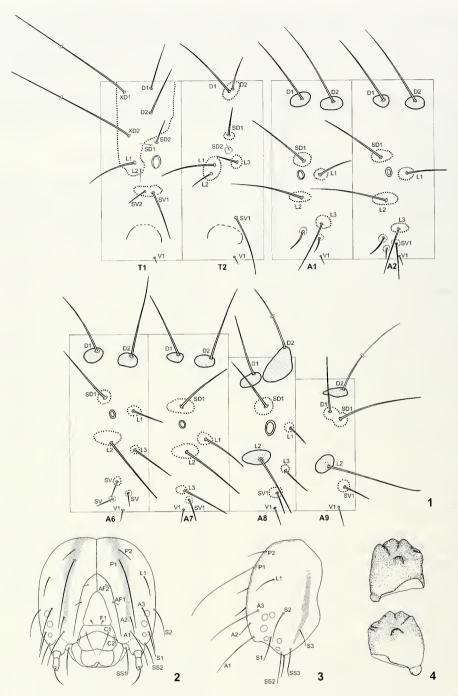
Descriptions of the living larvae are based on 42 images of C. cerintha from four different collections of wild larvae from Connecticut and Massachusetts and 20 images of C. cora larva from two collections of wild larvae from Florida and Ontario. Additionally, Cerma larvae were compared to images of 664 other North American Noctuidae sensu lato Franclemont and Todd (1983), including 7 genera and 53 species of Acronictinae, housed at the University of Connecticut.

A single *C. cerintha* larva was prepared for SEM study by running it through a series of ethanol baths (70%, 80%, 90%, 95%, 100%) before it was placed in a Polaron E 3000 critical point drying apparatus. The caterpillar was then coated with gold-palladium for three minutes in a Polaron E 5100 sputter coater. Images were obtained with a Zeiss DSM-982 Gemini FE SEM at 3–4 ky.

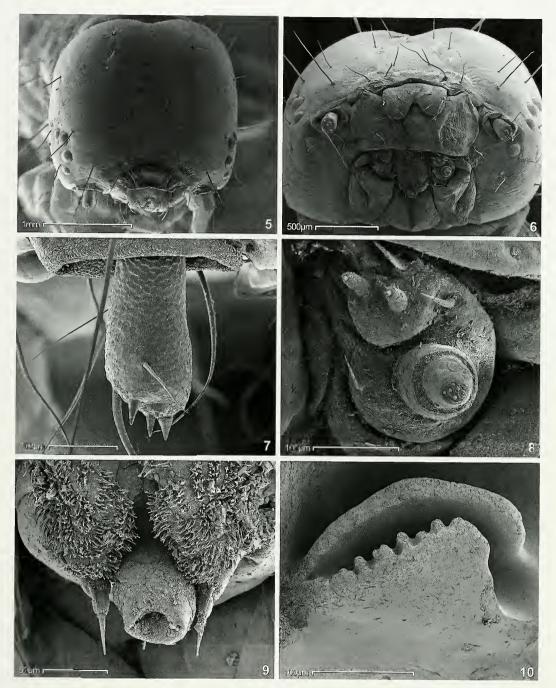
DESCRIPTION

Last instar of Cerma cerintha.---Length of preserved individuals: 28-31 mm (n=4). Initially bright lime to emerald green; integument shiny. Body wall translucent with tracheal trunk visible. Body constricted between segments (in preserved larvae). Setae long, thickened, mostly black, often from enlarged pinacula. Dorsum cherry red to smoky maroon with broad white subdorsal stripe from T1 to anterior of A8; stripe narrowing and more likely to include yellow pigment at either end of body. A8-A10 with broad white lateral line that dodges or is broken about spiracle on A8; lateral line subtended by narrow cherry red patch on A8-A9 with ray extending forward across A7 and down outer face of anal proleg. Spiracles pale orange. Middle instars lack brick red color over dorsum and each lobe of head draws to a point that bears a single black, bladelike seta. Prepupal larva tending towards glaucous green, dull, with reddish cast to lateral areas and subdorsal stripe with pink tints; noticeably thickened through the abdominal segments; dorsum fading to smoky maroon.

Head (Figs. 2–11): Smooth with long, thickened bristlelike setae; secondary setae absent. Capsule high relative to both depth (length) and width (Fig. 5); dark band extending from vertex down toward antenna but ending above A1 and second narrower band beginning under L seta and extending forward along gena, ending below ocellus 6. Triangle short, only about $0.4 \times$ height



Figs. 1–4. *Cerma cerintha* larva. 1, Last instar chaetotaxy map, T1–T2, A1–A2, and A6–A9. 2, Head, frontal. 3, Head, lateral. 4, Mandibles, mesal surfaces. SV2 and SV3 setae on A1 and A2 are unnumbered, in part because it appears that SV3 is missing on A1 whereas others (e.g., Kitching and Rawlins 1998) state that it is SV2 that is absent.



Figs. 5–10. Scanning electron micrographs of last instar *Cerma cerintha*. 5, Frontal view of head. 6, Mouthparts. 7, Antenna. 8, Maxilla. 9, Spinneret. 10, Mola.

of head; AF and, especially F, setae short. Clypeus (and anteclypeus) little more than twice wide as broad; anteclypeus furrowed; C1 twice length of C2.

P1, A3, and A1 very elongate, thickened, and brown. P1 extremely long, nearly height of head, circa $7 \times$ length of P2. Antenna as in Figs. 6, 7. Labrum somewhat quadrangular, deeply cleft. Maxilla as in Fig. 8. Mandible robust with three short teeth and central mola (Fig. 4); mola in end view consisting of two ridges; lower ridge with serrate margin (Fig. 10). Spinneret short, tubular, with apical pore, no dorsal groove, and no lateral flaps (Fig. 9). Hypopharyngeal spines extend to base of labial palpi (Fig. 9).

Body (Figs. 1, 11–17): Secondary setae absent. All dorsal setae including both XD on T1, L1 on T1, all L setae on T2– A9, and SV1 on all segments, very long, brown, thickened, more bristle-like than hair-like; D2 longer than D1 on abdominal segments. Dorsum between D2 pinacula covered by field of brown pavement granules (that appear rusty brown in preserved larvae). A8 humped.

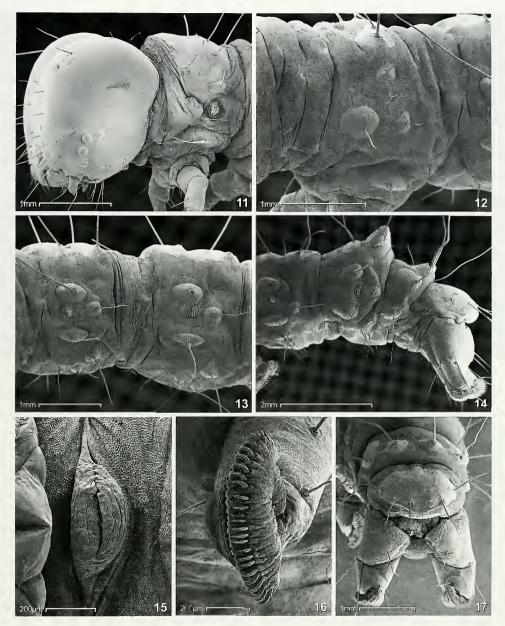
Thorax (Figs. 1, 11, 12, 15): Prothoracic shield undifferentiated (Fig. 11). XD1 and XD2 exceptionally long, approximately $5\times$ as long as D1. L1 and hair-thin L2 included on prothoracic shield. SD2 short and thin on T1–T3. Prominent, midventral cervical gland on A1 (Fig. 15). Legs long, subequal to height of segment that bears them.

Abdomen (Figs. 1, 13, 14, 17): D1 and D2 setae getting progressively longer caudad to A8. Similarly, dorsal pinacula larger, more melanized, and more elevated to A8; D2 pinaculum on A8 grossly enlarged and bearing body's longest seta-its length often greater than length of A8-A10. D2 seta on A9 also very long and borne from greatly enlarged pinaculum. D1 and SD1 pinacula fused on A9. SD2 highly reduced. L2 borne from enlarged sclerotized pinaculum on A8, $2 \times$ length of L1; single L2 seta on A9 borne from enlarged melanized pinaculum. Two SV setae on T1; 1 SV seta on T2-T3; 2 SV on A1; 3 on A2-A6; 1 on A7-A9; SV1 much longer than SV2 and SV3 on A2 (Figs. 1, 13). V setae closely approximate on T1, more distantly and progressively longer caudad. MD, MSD, and MV proprioreceptors very reduced (or absent) on the thoracic and abdominal segments. All prolegs present, slightly larger caudad; planta long, sometimes with reddishbrown plate along outer face (n=1/4). Crochets in a uniordinal mesoseries; crochet complement on A3–A6, A10: 26–29, 28–30, 31–32, 32–34, and 29–30, respectively (Fig. 16). Anal proleg well developed, longer than combined length of A9–A10 (Fig. 14), with elongate sclerotized plate on outer surface and smaller plate, roughly half length of former, along anterior surface.

Last Instar of Cerma cora.-Length of preserved individuals: 26-28 mm (n= 3). Aposematic; ground smoky with bright yellow (to orange) and white markings. Setae long, black, borne from enlarged blackened pinacula. A8 strongly humped. White middorsal stripe nearly continuous on thorax; broken over abdomen, usually expressed anterior to D1 and posterior to D2 pinacula. Broad white, lateral band running between D2 and L2 pinacula heavily suffused with bright yellow and orange, especially on A1-A8; yellow and/or orange spilling onto T3 and A9 in some individuals. A9 mostly white with boldly contrasting pinacula. Abdominal prolegs with shiny black plate along outer surface. Spiracles black. Thoracic legs shiny black. Head black, except for gray-white frons and adfrontal areas; lower half of frons also pale.

DISCUSSION

Last instars of *Cerma cerintha* and *C. cora* are readily distinguished from one another: *C. cerintha* is green with a brick red dorsum; *C. cora* is an aposematically-colored insect, mostly black with yellow and white markings. In *C. cora*, all the large setae of the thorax and abdomen are borne from blackened pinacula, the setae are generally longer and more darkly pigmented, and the



Figs. 11–17. Scanning electron micrographs of last instar *Cerma cerintha*; head to left. 11, Head and T1. 12, T3. 13, A1–A2. 14, A7–A10. 15, Cervical gland on venter of T1. 16, Crochets on A3. 17, Caudal segments.

prolegs on A3–A7 bear a strongly melanized plate. D1 and D2 are subequal in length in *cerintha*, while D2 is half again as long as D1 in *cora*. The D pinacula are fused on T2 and approximate over T3 in *C. cerintha*; but well separated on both T2 and T3 in *cora*. Larval characters shared by *C. cerintha* and *C. cora* that reinforce their congeneric status include the presence of a field of brownish dorsal pavement granules from (at least) T2 back to A9; deep constrictions between segments (in preserved larvae); exceptionally long,

strongly-pigmented, thickened primary setae, the longest being P1 on the head, XD1 and XD2 on T1, and D2 on A8 and A9. with latter often exceeding the combined length of A8-A10; elongated planta, nearly as long as the segment that bears it on A3-A6, and the absence of secondary setae. The degree to which the D2 pinaculum is enlarged on A8 in both insects is exceptional. A significant synapomorphy for the two species is the reduction of the SD2 seta on the abdominal segments and the MD. MSD, and MV proprioreceptors on the thoracic and abdominal segments. In addition, the cervical gland on **T1** (Fig. 15) appears to be well developed in the larvae of both Cerma. Finally, both feed on woody members of the Rosaceae, especially Crataegus, Prunus, and related species (Tietz 1972; Robinson et al. 2002).

LINKAGES TO ACRONICTINAE

Larval characters exclude Cerma from membership in either the Acontiinae or Eustrotiinae, the two subfamilies in which the genus has most recently resided (Franclemont and Todd 1983; Covell 2005, and Fibiger and Lafontaine 2005). Prolegs are absent on A3 and sometimes A4 in the former subfamily and from A3 in the latter subfamily. Cerma has a full complement of prolegs. No Acontiinae or Eustrotiinae possess long, thick, pigmented setae as do C. cerintha and C. cora. Cerma have prominent, raised pinacula, with those on A8 (especially the D2 pinacula) grossly enlarged-similar pinacula are not present in acontiines or eustrotiines. Acontiines have greatly thickened setae on the anal plate (Crumb 1956)—no such setae are present in Cerma.

While it is clear that *Cerma* is neither an acontiine nor eustrotiine, the argument that *Cerma* is an acronictine is weaker. *C. cerintha* and *C. cora* lack the most commonly identified features to circumscribe acronictines: verrucae, secondary setae, and the presence of extra setae on the L3 pinaculum on A1-A8 (Crumb 1956; Kitching and Rawlins 1998; Beck 1999, 2000). One character linking Cerma to acronictines (and arctiids) is the fusion of the dorsal pinacula over T2 and near fusion of the dorsal pinacula on T3 (in C. cerintha only). Based on my collections of noctuid larvae and larval images (representing 664 species of North American Noctuidae), Cerma shows greatest similarity to members of the Acronictinae, and in particular Acronicta fragilis (Guenée) and Harrisimenna trisignata (Walker). proportions, posture, setal Habitus girths and lengths, and development of the dorsal pinacula are reminiscent of those of A. fragilis.

Harrisimenna and Cerma share a number of similarities: both have thickened, darkly-pigmented dorsal setae that are borne from enlarged, black, pimplelike pinacula (Figs. 18-21). In C. cora and H. trisignata, A2 is modestly swollen laterally and dorsally-this segment has the widest girth of any of the anterior body segments; A1 and A3 are somewhat smaller in girth; all three segments have a greater circumference than that of T3. The eighth abdominal segment bears an enormous dorsal hump in H. trisignata, a prominent dorsal hump in C. cora, but only a low swelling in C. cerintha (at the midline, A8 is about $0.2 \times$ higher than the height of A9). In C. cora and H. trisignata, A8 is arched high above the adjacent segments. The planta is unusually long in both genera-in Cerma, the height of the planta is subequal to that of the segment from which it issues on A3-A6 (Fig. 21). The planta of Harrisimenna is also elongate (Fig. 20). In describing H. marmarota Hampson, an East Asian species, Yamamoto and Sugi (1987) noted that it possessed "extraordinary [sic] long prolegs." Additionally, the planta bears a strongly

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Figs. 18–21. Last instars of *Cerma* and *Harrisimenna*. 18, *C. cerintha*. 19, *C. cora*. 20, Defensive posture of *H. trisignata*. As is commonly the case in *Harrisimenna*, a previously shed head capsule is adhering to the caterpillar's prothoracic setae. 21, Defensive posture of *C. cora*. Note display of long black thoracic legs in both.

melanized (armored) plate on A3–A6 in *H. trisignata* and *C. cora* (but only 1 of 4 of the *C. cerintha* larvae examined). Both *Cerma* and *Harrisimenna* possess stout, armored anal prolegs with an elongate sclerotized plate running along the outer face on the proleg and a smaller sclerite along the anterior face of the proleg. At rest the long anal prolegs splay outward behind the body in each.

Both genera share similarities in their alarm responses. An extremely rapid (blurring) side-to-side shaking response occurs in both *Harrisimenna trisignata* and *Cerma cerintha*. A shared alarm posture has been observed in larvae of *H. trisignata* and both *Cerma* species: disturbed larvae arch the head up and back and extend the long, often blackened, thoracic legs outward (Figs. 20–21) (*H. trisignata* may also lift the caudal

segments). This posture exposes the larva's cervical gland (Fig. 15) located between the prothoracic coxae. (Presumably this posture and the aposematic coloration of C. cora larvae will be found to be functionally linked to a defensive secretion released from the gland). In the preserved specimens of both Cerma (n=9) and *Harrisimenna* (n=4) a portion of the gland is everted. This 'spigot' is especially well developed in the latter genus, extending outward 1.6 mm from the venter of the thorax in last instars (nearly reaching the spinneret in some individuals). Although a cervical gland capable of discharging defensive secretions is known in notodontids (Weatherston et al. 1979; Attygalle et al. 1993) and the noctuid Spodoptera Guenée (Marti and Rogers 1988), and may prove to be part of the noctuoid groundplan, I expect that its development in *Cerma*, *Harrisimemna*, and other acronictines will be found to be elaborated relative to most noctuid lineages. The presence of a defensive secretion would explain the comparatively conspicuous perching behaviors of some *Acronicta* (e.g., *A. impleta* Walker, *A. morula* Grote &. Robinson, and *A. hasta* Guenée), which perch on leaf uppersides by day, and the bright 'warning' coloration of *Cerma cora* and other acronictines (e.g., *Acronicta oblinita* (J. E. Smith), *A. funeralis* G. & R., *A. longa* Guenée, and *Simyra henrici* (Grote) (see Wagner 2005).

Cerma, and three acronictine genera, *Comachara* Franclemont, *Harrisimenna*, and *Polygrammate* Hübner, tunnel deep into wood as prepupae (Wagner 2005; Wagner et al. 2006). In the case of *Harrisimenna*, the caterpillars can bore into solid woods, e.g., dry indoor fir molding (Pat Burkett personal communication). The enlarged hump over A8, elongate prolegs, and sclerotized plates on the anal prolegs of *Cerma* and *Harrisimenna* may be functionally related to the biomechanics of tunneling into wood.

The weight of the evidence suggests that Cerma, despite its exceptional chaetotaxy, is closely related to the acronictine genus *Harrisimemna*. The latter genus is unequivocally acronictine in nature: it possesses larval characters noted above as being characteristic of acronictines; it has acronictine forewing patterning; it shares a seemingly unique tunneling/ball-rolling behavior with the acronictine genera Comachara and Polygrammate (Wagner et al. 2006, unpublished data); and has been treated as an acronictine by all modern noctuid workers (e.g., Forbes 1954; Crumb 1956; Franclemont and Todd 1983; Yamamoto and Sugi 1987). The inclusion of Cerma in the Acronictinae, would negate the most widely cited larval characters believed to uniquely identify the subfamily (presence of secondary setae and presence of one or more extra setae on the L3 pinaculum). Other morphological and molecular data are needed to corroborate or refute the character evidence presented here. As importantly, if *Cerma* proves to be an acronictine, additional data will help to clarify the position of the genus within the subfamily.

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